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The annotated checklist of plant species that occur in the wetland habitats of Georgia (the Caucasus)

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Abstract

The checklist includes 270 species that belong to 80 families and 183 genera. Each species has been annotated with the following information: life form, wetland indicator status, and location. In this checklist, Angiosperms are represented by 252 species (93.3%), Bryophytes – 10 species (3.7%), Pteridophytes – 8 (3%), Gymnosperms – 1 (0.4%). The largest families by the number of species are Cyperaceae – 39 (14.4%), Poaceae – 29 (10.7%), Rosaceae – 19 (7.1%), Asteraceae – 17 (6.3%), Fabaceae – 11 (4.1%) and Juncaceae – 11 (4.1%). The checklist is dominated by 55 Palaearctic species (20.4%), followed by 46 Holarctic (17.1%), 31 Euro-Mediterranean (11.5%), 31 Cosmopolitan (11.5%), and 27 Euro-Siberian (10.03%) species. The endemism rate is 4.8%, and the proportion of invasive and naturalized plants is 8.5%. Obligate wetland plants, mainly belonging to the families Cyperaceae and Juncaceae, make up 34.2% of the floristic composition. This is the first comprehensive published checklist of the flora of Georgian wetlands, annotated with wetland indicator values.

Key words

Chorotypes, Floristic composition, Life Forms, Wetlands, Wetland Indicator Status

Introduction

Wetland ecosystems are considered a natural resource of global importance. They provide many valuable ecosystem services, among them flood protection, water quality improvement, and carbon dioxide sequestration. Wetlands are home to thousands of plant and animal species (Verhoeven et al. 2006; Ramsar Convention Secretariat 2013), including endemic, relict, and rare species (Suppl. material 1, figs 1–3). Furthermore, the aesthetic and recreational benefits of wetlands are also important (Suppl. material 2, figs 1–3). Hence, the preservation of this ecosystem is of the utmost importance (Hazeu et al. 2010; Tedoradze et al. 2020). Many wetlands are threatened by eutrophication (Suppl. material 2: fig. 4) driven by both global and local factors, as well as habitat fragmentation and degradation (Verhoeven et al. 2006). Wetlands harbor many characteristic species, such as hydrophytes (Suppl. material 3, figs 1–2), which are often used as specific indicators for assessing the current condition of wetlands (Reed and Peters 1988; Lyon and Lyon 2011; Eggers and Reed 2015). Therefore, having a comprehensive checklist of wetland flora is the first necessary step for planning and executing the monitoring and conservation of wetlands in Georgia.

Georgia is a mountainous country adjacent to the sea, and such settings create steep climatic gradients, in which geographical location plays an important role (Kikvidze 2020). Therefore, we also performed a gradient analysis

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of the species composition of wetland communities across Georgia using geographical coordinates and altitude as environmental variables.

Here we present the recorded and assessed 270 species as a list of plants found in different wetlands in most regions of Georgia. It should be noted that number of studies have been published on wetlands in Georgia, relating to different periods (Kimeridze 1966, 1985; Melia 1985; Kikvidze and Oshawa 2001; Denk et al. 2001; BSSGW 2008; Matchutadze 2008; Krebs et al. 2009; Matchutadze et al. 2015). However, there are practically no studies covering all the major wetlands, nor do we have any studies on the indicator status of typical wetland species recorded. Therefore, our study addresses these two needs.

Materials and methods

Georgia is a climatically diverse country owing to the adjacent Black Sea and high mountain chains of various orientations. Through our sampling regions, the mean annual temperature varies from 14 °C in Colchis to 3 °C in Kazbegi; annual precipitation varies roughly between 600 and 900mm and its distribution changes from almost ideally uniform in Imereti (760mm ± 15SD) to strongly seasonal in Sioni (812mm ± 45SD). Therefore, the study regions represent quite a diverse climatic character (Fick and Hijmans 2017).

Study regions are located at different hypsometric heights and in different climatic zones. In total, we sampled 218 plots in seven regions across Georgia (Fig. 1): Kolkheti Lowland (121 plots), Javakheti Plateau (53 plots), mountainous Adjara – the highlands of Adjara (8 plots), Kazbegi region (7 plots), Iori River Gorge – the northwestern part of Kakheti province (9 plots), Upper Imereti (6 plots), Shida Kartli Lowland (6 plots), and Alazani Valley (8 plots).

Fieldwork campaigns were conducted during the vegetation seasons of 2015-2017. The sampling locations were selected prior to our fieldwork using topographic maps of the Soviet period (1950-60s), which depicted mires, swamps, and other wetlands in a rather detailed manner. Before sampling, we determined the location and morphology of wetland bodies with 5m accuracy using RapidEye satellite multispectral imagery.

Sampling points on the pre-selected sites were located using navigation instruments – GPS and satellite images. First, we described the hydrological conditions of a given wetland by assessing its water surface: water not visible (0), well visible (1), and partly visible (2); we also assessed observable human impacts through three categories (low, intermediate, and high impacts).

Vegetation was sampled as follows: once a wetland was recognized and inspected, the team chose visually the most representative area(s) for sampling. A central point of circular plots was placed at random in a selected area, and radii for plots were delineated: a 9 meter-radius circular plot around a sampling point was used to sample trees; a 6 meter-radius plot was used for sampling shrubs, and a 3 meter-radius circle was used for sampling herbaceous plants (USACE 1987). Within these plots, we identified and recorded all detectable species and assessed their abundance by the modified scale of Braun-Blanquet (r, +, 1, 2m, 2a, 2b, 3, 4, 5) (Braun-Blanquet 1964; van der Maarel 2007). Plant species were identified using the Key to Plants of Georgia (Ketskhoveli et al. 1964, 1969) and the Excursion Flora of Germany (Exkursionsflora von Deutschland) (Jäger et al. 2013). The plant species that were not easily identifiable in the field were collected and later accurately identified by comparing them to the specimens in the National Herbarium (TBI) of the Institute of Botany, Ilia State University, Georgia.

In all, we collected 216 herbarium specimens of 132 plant species (herbarium specimens will be available at the TBI). Latin names of taxa (families, genera, and species) are based on nomenclatural checklists of 'Flora of Georgia' (Gagnidze 2005; Davlianidze et al. 2018) and are harmonized with international plant databases (Euro+Med 2006; GBIF 2022; IPNI 2022; POWO 2022; WFO 2022). Species that are alien to Georgia are listed according to Kikodze et al. (2010).

Each species was ranked according to its wetland indicator status on the following scale (USACE 1987; Reed and Peters 1988; Lyon and Lyon 2011; Lichvar et al. 2013; Eggers and Reed 2015):

- Obligate wetland plants (OBL) – almost always occur in wetlands (estimated probability > 99%) under natural conditions.
- Facultative wetland plants (FACW) – usually occur in wetlands (estimated probability 67% – 99%), but is occasionally found in non-wetlands.
- Facultative plants (FAC) – equally likely to occur in wetlands (estimated probability 34% – 66%) or non-wetlands.
- Facultative upland plants (FACU) – usually occur in non-wetlands (estimated probability 67% – 99%), but are occasionally found in wetlands (estimated probability 1% – 33%).
- Obligate upland plants (UPL) – almost always occur (estimated probability > 99%) in non-wetlands under natural conditions.

Each species was assessed for its phytogeographical distribution (Komarov 1934-1960; Takhtajan 1954-2011, 2003-2012; Tutin et al. 1964-1993; Davis 1965-2001; Ketskhoveli et al. 1971-2011) and online international plant databases (GBIF 2022; Euro+Med 2006; POWO 2022). In addition, we used different regional works in this field to determine the chorotypes of the species (Gagnidze and Kemularia-Nathadze 1985; Portenier 1993, 2000; Gagnidze 2004; Shetekauri and Chelidze 2016; Lachashvili et al. 2020; Lachashvili et al. 2021; Tedoradze 2022). Plant life forms were determined using the LEDA Traitbase (Klotz et al. 2002). Endemics of the Caucasus are given after Solomon et al. (2013).

To analyze the variation of species composition on geographical gradients, we performed Canonical Correspondence Analysis (CCA). Statistical significance was computed with 999 permutation tests. We analyzed species with a frequency of occurrence in the community matrix equal to or greater than 5. For this purpose, we used PAST (v. 4.12) software (Hammer et al. 2001).

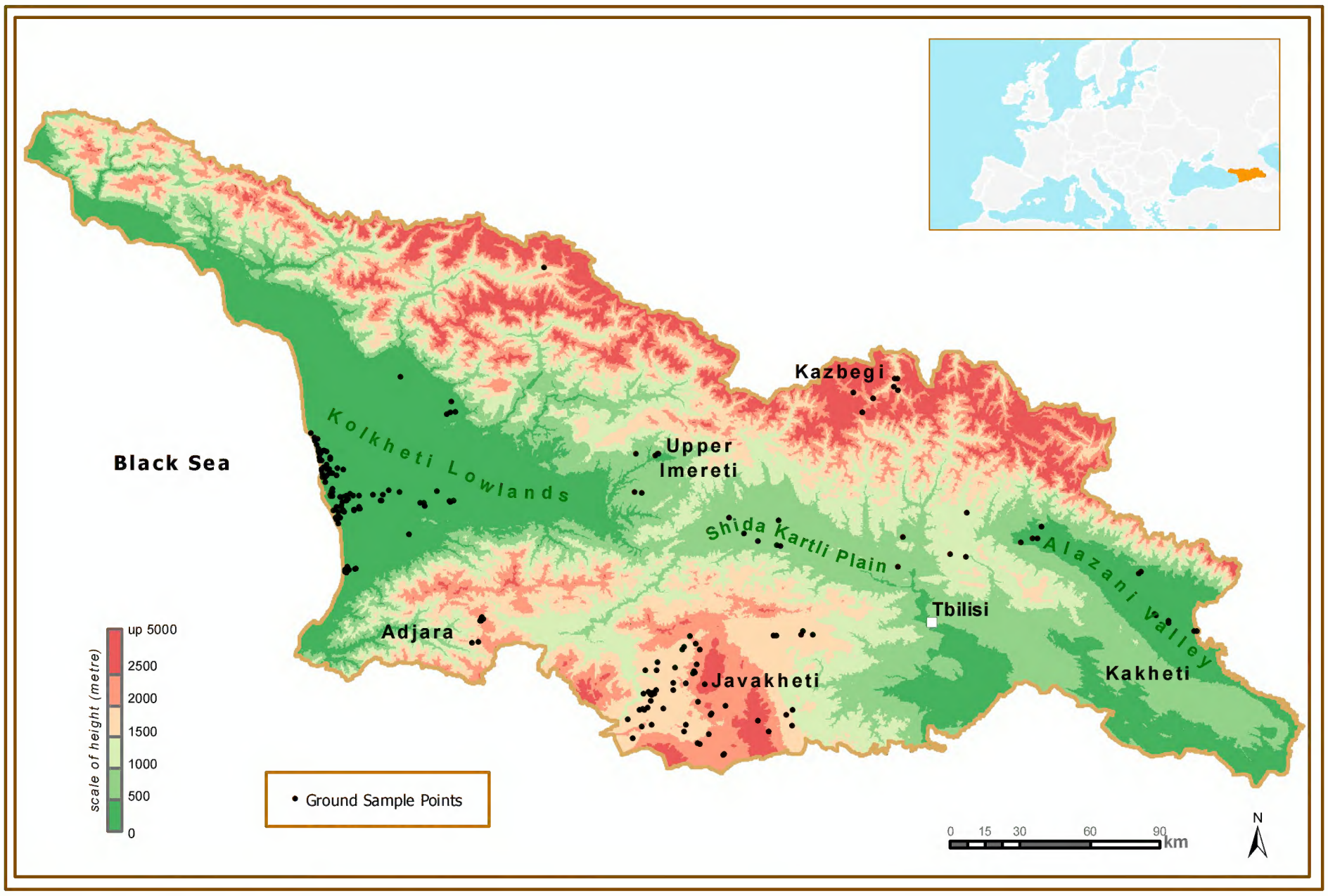

Figure 1. Map showing study sites/plots in Georgia.

Results and discussion

We sampled wetlands across the diverse landscapes of Georgia: the Black Sea coastal zone with a maritime climate, the inland lowlands with a dry and continental climate, high dry plateaus, and subalpine environments. Our results permitted us to construct an annotated checklist of the wetland flora of Georgia, which includes 270 species sampled from 218 pre-selected sites. Each species on the resulting checklist (Table 1) is annotated with the following data: life form, wetland indicator status, chorotype, and location (study regions). The coordinates of each plot can be found in the supplementary information, where the species presence-absence matrix is also included as Suppl. material 4.

The checklist includes 270 species belonging to 80 families and 183 genera. Angiosperms are the core of the floristic composition – 251 species (93%). Bryophytes are represented by 10 species (3.7%), Pteridophytes – 8 (3%), Gymnosperms – 1 (0.4%). Leading families by the number of species are Cyperaceae – 39 (14.4%), Poaceae – 29 (10.7%), Rosaceae – 19 (7.1%), Asteraceae – 17 (6.3%), Fabaceae – 11 (4.1%) and Juncaceae – 11 (4.1%). The floristic composition of Georgian wetlands is dominated by Palaearctic species 55 (20.4%), followed by Holarctic 46 (17.1%), Euro-Mediterranean 31 (11.5%), Cosmopolitan 31 (11.5%) and Euro-Siberian 27 (10.03%) species.

Out of 270 species, half are represented by only one or two sites. The most frequent species are *Alnus glutinosa* subsp. *barbata* – (69 sites), *Molinia caerulea* – (56 sites), *Juncus effusus* – (42 sites), *Carex vesicaria* – (40 sites), *Phragmites australis* – (37 sites), *Persicaria thunbergii* – (36 sites), *Sphagnum palustre* – (35 sites), *Lythrum salicaria* – (32 sites), *Cladium mariscus* – (29 sites), *Frangula alnus* – (29 sites). Among the species listed above, five are OBL in wetlands, three – FACW, and of the remaining two, one – FACU and the other – FAC. The presence of the latter, among the ten most frequent species, indicates the current state of the wetland, which is often expressed by fragmentation and the spread of species uncharacteristic for wetlands.

The percent share of endemic species in the checklist is 4.8 %; the rate of endemism is low compared to the flora of Georgia, where the endemism rate is approximately 31% (Solomon et al. 2013). There are 13 endemic species, four of which are endemic to Georgia and nine to the Caucasus. At the same time, we recorded 23 non-native species, which gives a rate (8.5%) higher than that of endemics. The low endemism rate in wetland vegetation is not surprising since the typical wetland species usually have a very wide distribution; wetland vegetation is often considered to be azonal (sensu Sieben 2019), with very little variable composition across large gradients within subcontinents such as Mexico (Ramos-Tapia et al. 2022) or South Africa (Mucina et al. 2006) or even between so distant places such as the western and eastern extremities of Eurasia (Kikvidze and Ohsawa 2001; see also Denk et al. 2001).

In the checklist, species that almost always occur in wetlands (OBL) and species that are commonly (FACW) found in wetlands together made up 52.1% of the total number of species (OBL – 92 and FACW – 48 species). Species that are equally likely to occur in wetlands or non-wetlands (FAC) made up 68 species (25.3%). The plants that usually occur in non-wetlands but are occasionally found in wetlands (FACU) consisted of 62 species (23.1%).

Table 1. Annotated checklist of plant species that occur in the wetland habitats of Georgia. **LF** (Life Forms): F – Ferns; H – Herbaceous; H(A) – Herbaceous (Aquatic); M – Moss; W – Woody; W(L) – Woody (Liana). **WIS** (Wetland Indicator Status): FAC – Facultative; FACU – Facultative upland; FACW – Facultative Wetland; OBL – Obligate. **Chorotypes**: Aus. – Native Australia; CA – Caucaso-Anatolian; Cau. – Caucasian; Cau.(EC) – Caucasian (Endemic of Caucasia); Cau.(EG) – Caucasian (Endemic of Georgia); CE – Caucaso – Euxinian; Cosm. – Cosmopolitan; Cosm.(ExPR) – Cosmopolitan (except polar regions.); Cosm.(MO) – Cosmopolitan/Mediterranean origin; Cosm.(SAmI) – Cosmopolitan/South America origin/invasive; Cosm.(TAf) – Cosmopolitan/Probably native to tropical Africa; CSWA – Caucaso-SW Asian; E – European; EA – East Asian; EA(I) – East Asian/invasive; EA(N) – East Asian/naturalized; EMed. – Euro-Mediterranean; EMed.(Cond.) – Euro-Mediterranean conditionally; ES – Euro-Siberian; ESWA – Euro-SW Asian; Eux. – Euxinian; HE – Hyrcano-Euxinian; Hol. – Holarctic; IT – Irano-Turanian; Med. – Mediterranean; Med. (Cond.) – Mediterranean conditionally; MSWA – Mediterranean-SW Asian; MSWAES – Med.-S.W. As.-Euras. Steppe; NA – North American; NA(Adv) – North American/adventive; NA(I) – North American/invasive; NA(N) – North American/naturalized; Pal. – Palearctic; Pal.(W) – West Palearctic; Pal.(WW) – Palearctic/worldwide introduced; SA(N) – S American/naturalized; SEA – SE Asian; **Study Regions in Georgia**: 1 – Kolkheti lowland; 2 – Javakheti; 3 – Mtiani Adjara; 4 – Mtiuleti; 5 – Iori River gorge; 6 – Upper Imereti; 7 – Shida Kartli lowland and Alazani Valley.

Family	Species	LF*	WIS**	Chorotypes	Study Regions in Georgia
Bryophyta					
Brachytheciaceae	*Brachythecium mildeanum* W. P. Schimper	M	OBL	Pal.	1
Climaciaceae	*Climacium dendroides* Weber & D. Mohr	M	OBL	Hol.	3
Mniaceae	*Plagiomnium ellipticum* T.Koponen	M	OBL	Hol.	3
Polytrichaceae	*Polytrichastrum longisetum* G.L. Smith	M	OBL	Hol.	3
	Polytrichum strictum Menzies ex Bridel	M	OBL	Hol.	3
Sphagnaceae	*Sphagnum capillifolium* Hedwig	M	OBL	Cosm.	1,3
	Sphagnum imbricatum Hornschuch ex Russow	M	OBL	Pal.	1,3
	Sphagnum palustre L.	M	OBL	Cosm.	1,3
	Sphagnum papillosum Lindberg	M	OBL	Hol.	1
	Sphagnum platyphyllum Warnstorf	M	OBL	Hol.	1
Pteridophyta					
Aspleniaceae	*Asplenium trichomanes* L.	F	FACU	Cosm.	1
Athyriaceae	*Athyrium filix-femina* (L.) Roth	F	FAC	Hol.	1
Dennstaedtiaceae	*Pteridium aquilinum* (L.) Kuhn (*P. tauricum* V. I. Krecz.)	F	FAC	Pal.	1
Dryopteridaceae	*Dryopteris filix-mas* (L.) Schott	F	FAC	Hol.	7
Equisetaceae	*Equisetum palustre* L.	H	FACW	Hol.	1,2,3,4,5,6,7
Lycopodiaceae	*Lycopodiella inundata* (L.) Holub (*Lycopodium inundatum* L.)	F	OBL	Hol.	4
Osmundaceae	*Osmunda regalis* L.	F	OBL	EMed.	1
Salviniaceae	*Salvinia natans* (L.) All.	F	OBL	Pal.(WW)	1,7
Gymnospermae					
Pinaceae	*Pinus pinaster* Aiton (*P. maritima* Du Roi)	W	FAC	Med.	1
Angiospermae					
Dicotyledonae					
Apiaceae	*Anthriscus sylvestris* (L.) Hoffm.	H	FACU	Pal.	4
	Carum carvi L.	H	FACU	Pal.	3
	Daucus carota L.	H	FACU	Pal.(W)	5
	Eryngium caeruleum M.Bieb.	H	FACU	IT	5
	Eryngium campestre L.	H	FACU	EMed.	1
Apocynaceae	*Periploca graeca* L.	W(L)	FACW	EMed.	1,7
	Vinca major subsp. *hirsuta* (Boiss.) Stearn (*V. pubescens* D'Urv.)	H	FAC	CA	1
Aquifoliaceae	*Ilex colchica* Pojark.	W(L)	FAC	Eux.	1
Araliaceae	*Hydrocotyle ramiflora* Maxim.	H	OBL	EA	1,3
	Hydrocotyle vulgaris L.	H	OBL	EMed.	1
	Hedera colchica (K.Koch) K.Koch	W(L)	FACW	CA	1
	Hedera helix L.	W(L)	FAC	ES	1,7
Asteraceae	*Achillea millefolium* L.	H	FACU	Hol.	2
	Ambrosia artemisiifolia L.	H	FACU	NA(I)	1
	Arctium lappa L.	H	FAC	Pal.	2,5
	Artemisia absinthium L.	H	FAC	Pal.	2
	Bidens tripartita L.	H	OBL	Hol.	1,3,5
	Centaurea oxylepis (Wimm. & Grab.) Hayek	H	FACW	EMed.	1
	Cichorium intybus L.	H	FACU	Cosm.	2,6
	Cirsium arvense (L.) Scop.	H	FACU	Cosm.	5
	Cirsium obvallatum (M.Bieb.) M.Bieb. (*C. obvallatum* (M.Bieb.) Fisch.)	H	FACU	Cau.	4
	Cirsium vulgare (Savi) Ten.	H	FACU	Cosm.	2
	Eupatorium cannabinum L.	H	FACW	EMed.	1,5
	Inula helenium L.	H	FAC	Pal.(W)	5
	Pentanema britannicum (L.) D.Gut.Larr., Santos-Vicente, Anderb., E.Rico & M.M.Mart.Ort. (*Inula britannica* L.)	H	FACW	ES	2,5
	Petasites albus (L.) Gaertn.	H	FACW	E	2
	Solidago canadensis L.	H	FACU	NA(N)	1,7
	Taraxacum campylodes G.E.Haglund (*Leontodon taraxacum* L.; *Taraxacum officinale* Weber ex Wiggins)	H	FACU	Pal.	2

Family	Species	LF*	WIS**	Chorotypes	Study Regions in Georgia
	Xanthium strumarium L.	H	FAC	Cosm.	1
Betulaceae	*Alnus glutinosa* subsp. *barbata* (C.A.Mey.) Yalt. (*A. barbata* C.A.Mey.)	W	FACW	Cau.(EC)	1,5,7
	Carpinus betulus L. (*C. caucasica* Grossh.)	H	FACU	EMed.	1
	Corylus avellana L.	H	FACU	EMed.	1,7
Brassicaceae	*Capsella bursa-pastoris* (L.) Medik.	H	FACU	Cosm.	1,2
	Nasturtium officinale R.Br.	H	OBL	Cosm.	4
Caprifoliaceae	*Cephalaria gigantea* (Ledeb.) Bobrov	H	FACU	Cau.	2
	Dipsacus laciniatus L.	H	FACU	ESWA	5
	Valeriana alliariifolia var. *tiliifolia* (Troitsky) V.E.Avet. (*V. tiliifolia* Troitsky)	H	FAC	Cau.(EG)	5
Celastraceae	*Euonymus europaeus* L.	H	FAC	EMed.	1,2,5
Ceratophyllaceae	*Ceratophyllum demersum* L.	H(A)	OBL	Cosm.	2
Convolvulaceae	*Convolvulus arvensis* L.	H	FAC	Pal.	1,5
Cornaceae	*Cornus sanguinea* subsp. australis (C.A.Mey.) Jáv. (*Swida australis* (C. A. Mey.) Pojark. ex Grossh.)	W	FAC	Eux.	1,5,7
Droseraceae	*Drosera intermedia* Hayne	H	OBL	Hol.	3
	Drosera rotundifolia L.	H	OBL	Hol.	1
Ebenaceae	*Diospyros lotus* L.	W	FAC	SEA	1
Elaeagnaceae	*Elaeagnus angustifolia* L.	W	FAC	Pal.	7
	Hippophae rhamnoides L.	W	FAC	Pal.	4
Ericaceae	*Rhododendron luteum* Sweet	W	FAC	Eux.	1
	Rhododendron ponticum L.	W	FAC	Eux.	1
	Vaccinium arctostaphylos L.	W	FACW	CA	1
Fabaceae	*Amorpha fruticosa* L.	W	FACW	NA(I)	1,5
	Colutea orientalis Mill.	W	FACU	CSWA	5
	Gleditsia triacanthos L.	W	FAC	NA(N)	1
	Glycyrrhiza glabra L.	H	FACU	Pal.(W)	5,7
	Ononis arvensis L.	W	FAC	Pal.(W)	5
	Robinia pseudoacacia L.	W	FACU	NA(I)	1
	Trifolium canescens Willd.	H	FACU	CSWA	2
	Trifolium pratense L.	H	FAC	Pal.	2,4
	Trifolium repens L.	H	FAC	Pal.	1
	Trifolium spadiceum L.	H	FACW	ES	4
	Vicia tenuifolia subsp. *variabilis* (Freyn & Sint.) Dinsm. (*V. variabilis* Freyn & Sint.)	H	FACU	CSWA	1,5
Fagaceae	*Quercus hartwissiana* Steven	W	FAC	Eux.	1
	Quercus petraea subsp. *iberica* (Steven ex M. Bieb.) Krassiln. (*Q. iberica* Steven)	W	FACU	CSWA	5
Gentianaceae	*Gentiana septemfida* Pall.	H	FAC	CA	4
	Swertia iberica Fisch. ex C.A. Mey.	H	OBL	Cau.(EG)	4
Hypericaceae	*Hypericum mutilum* L.	H	FACW	NA(N)	1,2
	Hypericum perforatum L.	H	FACU	Pal.	1
Juglandaceae	*Pterocarya fraxinifolia* (Poir.) Spach (*Juglans pterocarpa* Michx.)	W	FACW	HE	1,7
Lamiaceae	*Lycopus europaeus* L.	H	OBL	ES	1,2
	Mentha aquatica L.	H	OBL	Cosm.	1,7
	Prunella vulgaris L.	H	FACU	Hol.	1
	Stachys palustris L.	H	OBL	ES	1,6
	Thymus collinus M.Bieb.	H	FACU	Cau.(EC)	2,5
Lentibulariaceae	*Utricularia minor* L.	H	OBL	Hol.	1
	Utricularia vulgaris L.	H	OBL	Pal.	2
Lythraceae	*Lythrum hyssopifolia* L.	H	OBL	Cosm.	5
	Lythrum salicaria L.	H	OBL	Pal.	1,2,4,5,6,7
	Trapa natans L. (*T. colchica* Albov)	H(A)	OBL	Pal.	1
Malvaceae	*Hibiscus coccineus* (Medik.) Walter	H	FAC	NA(I)	1
	Hibiscus ponticus Rupr.	H	FACW	Cau.(EG)	1
	Kosteletzkya pentacarpos (L.) Ledeb.	H	FACW	EMed. (Cond.)	1
Menyanthaceae	*Menyanthes trifoliata* L.	H	OBL	Hol.	1,2,3
Moraceae	*Ficus carica* L.	W	FACU	IT	1
	Morus alba L.	W	FAC	EA	7
	Morus nigra L.	W	FAC	ESWA	1,7
Myrtaceae	*Eucalyptus cinerea* F.Muell. ex Benth.	W	FACW	Aus.	1
Nymphaeaceae	*Nuphar lutea* (L.) Sibth. & Sm.	H(A)	OBL	ES	1
	Nymphaea alba L.	H(A)	OBL	EMed.	1,2
Oleaceae	*Fraxinus excelsior* L.	W	FACU	ES	1,7
Onagraceae	*Epilobium montanum* L.	H	FAC	ES	4
	Epilobium palustre L.	H	OBL	Hol.	2,4
Orobanchaceae	*Euphrasia caucasica* Juz.	H	FACU	Cau.(EC)	4
	Rhamphicarpa medwedewii Albov	H	FACW	Cau.(EC)	1
	Rhinanthus minor L.	H	FACU	ES	4
Parnassiaceae	*Parnassia palustris* L.	H	OBL	Hol.	4
Phytolaccaceae	*Phytolacca americana* L.	H	FACU	NA	1,7

Family	Species	LF*	WIS**	Chorotypes	Study Regions in Georgia
Plantaginaceae	*Plantago major* L.	H	FAC	Hol.	7
	Plantago media L.	H	FAC	Pal.	2
Polygonaceae	*Persicaria hydropiper* (L.) Delarbre (*Polygonum hydropiper* L.)	H	OBL	Cosm.	3
	Persicaria maculosa Gray (*Polygonum persicaria* L.)	H	FACW	Pal.	1,2,6
	Persicaria perfoliata (L.) H.Gross (*Polygonum perfoliatum* L.)	H	FAC	EA(I)	1
	Persicaria thunbergii (Siebold & Zucc.) H.Gross (*Polygonum thunbergii* Siebold & Zucc.)	H	FACW	EA(I)	1,7
	Polygonum carneum K.Koch	H	FAC	CA	2
Primulaceae	*Lysimachia vulgaris* L.	H	FACW	Pal.	1,2,5
	Primula auriculata Lam.	H	FACW	CSWA	3
Ranunculaceae	*Clematis vitalba* L.	H	FAC	EMed.	1
	Ranunculus caucasicus M.Bieb.	H	FACU	Cau.(EC)	2
	Ranunculus ophioglossifolius Vill.	H	OBL	EMed.	2,5
	Ranunculus trichophyllus Chaix (*Batrachium trichophyllum* (Chaix) Bosch)	H	OBL	Hol.	2
Rhamnaceae	*Frangula alnus* Mill.	H	FAC	ES	1,7
	Paliurus spina-christi Mill.	H	FACU	MSWA	1
Rosaceae	*Agrimonia eupatoria* L.	H	FACU	Pal.(W)	1
	Alchemilla sericata Rchb.	H	FACU	Cau.(EC)	4
	Comarum palustre L.	H	OBL	Hol.	1,2,3
	Crataegus microphylla K.Koch	H	FAC	ESWA	1
	Crataegus monogyna Jacq. (*C. kyrtostyla* Fingerh. ex Schltdl.)	H	FACU	ES	1
	Filipendula vulgaris Moench	H	FACU	Pal.	2
	Fragaria vesca L.	H	FACU	Hol.	7
	Geum urbanum L.	H	FACU	Pal.(W)	1,7
	Malus sylvestris subsp. *orientalis* (Uglitzk.) Browicz (*M. orientalis* Uglitzk.)	W	FAC	CSWA	1
	Mespilus germanica L.	W	FAC	EMed.	1
	Potentilla erecta (L.) Raeusch.	H	FACU	ES	1,3
	Pyrus communis subsp. *caucasica* (Fed.) Browicz (*P. caucasica* Fed.)	W	FACU	Cau.	1
	Rosa canina L.	W	FACU	Pal.(W)	1
	Rubus caesius L.	W	FAC	Pal.(W)	1
	Rubus caucasicus Focke	W	FACU	Cau.(EC)	1
	Rubus caucasigenus (Sudre) Juz.	W	FAC	Cau.(EC)	1
	Rubus hirtus Waldst. & Kit.	W	FACU	EMed.	1
	Rubus silesiacus Weihe (*R. candicans* Weihe)	W	FAC	E	1
	Spiraea japonica L.f.	H	FACU	EA	1
Rubiaceae	*Galium verum* L.	H	FACU	Pal.	2
Rutaceae	*Citrus trifoliata* L.	H	FAC	EA	1
Salicaceae	*Populus* × *canescens* (Aiton) Sm.	W	FACW	ES	7
	Salix alba L.	W	FACW	ES	5,7
	Salix caprea L.	W	FAC	ES	5
Sapindaceae	*Acer campestre* L.	W	FACU	EMed.	1,4,7
	Acer negundo L.	W	FACW	NA(Ad)	7
Simaroubaceae	*Ailanthus altissima* (Mill.) Swingle	W	FACU	EA(I)	5
Solanaceae	*Solanum dulcamara* L. (*S. persicum* Willd.)	H	FACW	Pal.	1
Ulmaceae	*Ulmus minor* Mill.	H	FAC	EMed.	1,7
Urticaceae	*Urtica dioica* L.	H	FAC	Pal.	5,7
Viburnaceae	*Sambucus ebulus* L.	W	FAC	EMed.	7
	Sambucus nigra L.	W	FAC	EMed.	1
	Viburnum lantana L.	W	FACU	EMed.	1
	Viburnum opulus L.	W	FACW	ES	1,7
Monocotyledonae					
Acoraceae	*Acorus calamus* L.	H	OBL	Hol.	1
Alismataceae	*Alisma plantago-aquatica* L.	H	OBL	Pal.	1,2,3,4,5,6
	Sagittaria sagittifolia L.	H	OBL	ES	1,2
Amaryllidaceae	*Allium* sp.	H	FAC	-	5
	Pancratium maritimum L.	H	FACU	Med.	1
Araceae	*Lemna minor* L.	H(A)	OBL	Cosm.	2,3,6
	Lemna trisulca L.	H(A)	OBL	Cosm.	1,2
Asparagaceae	*Asparagus officinalis* L.	H	FACU	ES	1
	Ruscus aculeatus L.	W	FAC	EMed.	1
	Ruscus colchicus Yeo	W	FAC	Cau.(EC)	1
Butomaceae	*Butomus umbellatus* L.	H	OBL	Pal.	2
Commelinaceae	*Commelina communis* L.	H	FAC	EA(N)	1
Cyperaceae	*Blysmus compressus* (L.) Panz. ex Link	H	OBL	Pal.(W)	2,3,4
	Bolboschoenus maritimus (L.) Palla	H	OBL	Cosm.(ExPR)	1,5,7
	Carex acuta L.	H	OBL	ES	2
	Carex aterrima subsp. *medwedewii* (Leskov) T.V.Egorova (*C. medwedewii* Leskov)	H	FAC	CSWA	3
	Carex canescens L.	H	OBL	Hol.	1,2
	Carex cespitosa L.	H	OBL	ES	2

Family	Species	LF*	WIS**	Chorotypes	Study Regions in Georgia
	Carex diluta M.Bieb.	H	FACW	IT	4
	Carex disticha Huds.	H	OBL	EMed.	2,3
	Carex divulsa Stokes	H	FAC	EMed.	17
	Carex echinata Murray	H	OBL	EMed.	2,3
	Carex elata All.	H	OBL	EMed.	2,4
	Carex hirta L.	H	OBL	EMed.	2,4,5
	Carex lachenalii Schkuhr	H	OBL	Hol.	2
	Carex lasiocarpa Ehrh.	H	OBL	Hol.	1,2
	Carex leporina L.	H	OBL	ES	4
	Carex limosa L.	H	OBL	Hol.	2
	Carex muricata L.	H	FAC	ES	1
	Carex nigra subsp. *juncea* (Fr.) Soó (*C. juncella* (Fries) Th. Fries)	H	OBL	ES	3
	Carex nigra subsp. *transcaucasica* (T.V.Egorova) Jim.Mejías, G.E.Rodr.-Pal., Amini Rad & Martín-Bravo (*C. transcaucasica* T.V.Egorova)	H	OBL	CSWA	2
	Carex pallescens L.	H	FACW	Hol.	2
	Carex panicea L.	H	OBL	ES	1
	Carex pendula Huds.	H	FACW	EMed.	2
	Carex pseudocyperus L.	H	OBL	Hol.	2
	Carex riparia Curtis	H	OBL	EMed.	1,2,4
	Carex rostrata Stokes	H	OBL	Hol.	1,2,3
	Carex tristis M.Bieb.	H	FAC	CA	4
	Carex vesicaria L.	H	OBL	Hol.	1,2,3,4,7
	Cladium mariscus (L.) Pohl	H	OBL	Cosm.	1,2,7
	Cyperus flavescens L. (*Pycreus flavescens* (L.) P.Beauv. ex Rchb.)	H	FACW	Cosm.	1
	Cyperus longus subsp. *badius* (Desf.) Bonnier & Layens (*C. badius* Desf.)	H	FACW	Med. (Cond.)	3
	Cyperus pannonicus Jacq. (*Juncellus pannonicus* (Jacq.) C.B. Clarke)	H	FACW	Pal.	1
	Cyperus serotinus Rottb.	H	FACW	Pal.	1
	Eleocharis palustris (L.) Roem. & Schult.	H	OBL	Hol.	2,3
	Eleocharis uniglumis (Link) Schult.	H	OBL	Hol.	2
	Rhynchospora alba (L.) Vahl	H	OBL	Hol.	1
	Rhynchospora caucasica Palla	H	OBL	Cau.(EG)	1
	Schoenoplectiella mucronata (L.) J.Jung & H.K.Choi (*Scirpus mucronatus* L.)	H	FACW	Cosm.	1,2
	Schoenoplectus tabernaemontani (C.C.Gmel.) Palla (*Scirpus tabernaemontani* C. C. Gmel.)	H	OBL	Cosm.	2
	Scirpus sylvaticus L.	H	FACW	Pal.(W)	1,3,5
Hydrocharitaceae	*Elodea densa* (Planch.) Casp.	H(A)	OBL	SA(N)	1
	Hydrocharis morsus-ranae L.	H(A)	OBL	ES	1,7
Iridaceae	*Iris pseudacorus* L.	H	OBL	Pal.(W)	1,6,7
Juncaceae	*Juncus acutus* L.	H	FACW	EMed.	1
	Juncus articulatus L.	H	OBL	Hol.	1,2,4
	Juncus atratus Krock.	H	OBL	ES	2
	Juncus bufonius L.	H	FACW	Cosm.	1,3
	Juncus conglomeratus L.	H	OBL	Pal.(W)	2,3
	Juncus effusus L.	H	OBL	Cosm.	1,2,3,6,7
	Juncus filiformis L.	H	FACW	Hol.	2
	Juncus inflexus L.	H	FACW	Pal.(W)	4
	Juncus maritimus Lam.	H	FACW	EMed.	1
	Luzula multiflora (Ehrh.) Lej.	H	FACU	Hol.	2
	Luzula stenophylla Steud. (*L. pseudosudetica* (V.I.Krecz.) V.I.Krecz.)	H	FAC	CSWA	2
Juncaginaceae	*Triglochin palustris* L.	H	OBL	Hol.	4
Orchidaceae	*Spiranthes sinensis* (Pers.) Ames (*S. amoena* (M. Bieb.) Spreng.)	H	OBL	SEA	1
Poaceae	*Agrostis capillaris* L. (*A. tenuis* Sibth.)	H	FAC	Pal.	2
	Agrostis vinealis Schreb.	H	FAC	CA	2,5
	Alopecurus aequalis Sobol.	H	OBL	Hol.	2
	Alopecurus arundinaceus Poir.	H	FACW	Pal.	2
	Anthoxanthum odoratum L.	H	FAC	EMed.	2
	Beckmannia eruciformis (L.) Host.	H	FACW	Pal.	2
	Bromus variegatus M.Bieb. (*Bromopsis variegata* (M.Bieb.) Holub)	H	FACU	CSWA	4
	Calamagrostis arundinacea (L.) Roth	H	FAC	Pal.	2,5,7
	Calamagrostis epigejos (L.) Roth	H	FAC	ES	1,2,5
	Calamagrostis pseudophragmites (Haller f.) Koeler	H	FAC	Pal.	2
	Cynodon dactylon (L.) Pers.	H	FAC	Cosm.(TAf)	1,6,7
	Dactylis glomerata L.	H	FAC	Pal.	2
	Echinochloa crus-galli (L.) P. Beauv.	H	FACW	Cosm.	1
	Festuca drymeja Mert. & W.D.J. Koch	H	FAC	MSWA	7
	Koeleria luerssenii (Domin) Domin	H	FACU	Cau.	4
	Lolium rigidum Gaudin	H	FACU	MSWA	2
	Molinia caerulea (L.) Moench	H	FACU	Pal.(W)	1,2,6,7
	Nardus stricta L.	H	FACU	Hol.	2,3,4
	Oplismenus undulatifolius (Ard.) P.Beauv.	H	FACW	Cosm.	1,7

Family	Species	LF*	WIS**	Chorotypes	Study Regions in Georgia
	Paspalum dilatatum Poir.	H	FACW	Cosm.(SAmI)	1,6,7
	Paspalum distichum L.	H	OBL	SA(N)	1
	Phleum phleoides (L.) H. Karst.	H	FACU	Pal.	2
	Phleum pratense L.	H	FACU	Pal.	3,4
	Phragmites australis (Cav.) Trin. ex Steud.	H	FACW	Cosm.	1,2,4,5,6,7
	Poa annua L.	H	FAC	Pal.(WW)	4
	Scolochloa festucacea (Wild.) Link	H	OBL	Hol.	2
	Sorghum halepense (L.) Pers.	H	FAC	Cosm.(MO)	1
	Sporobolus fertilis (Steud.) Clayton	H	FACW	EA(I)	1
	Stipa pulcherrima K.Koch	H	FACU	MSWAES	2
Potamogetonaceae	*Potamogeton crispus* L.	H(A)	OBL	Cosm.	1,2
	Potamogeton natans L.	H(A)	OBL	Hol.	1,2
	Zannichellia palustris L.	H	OBL	Cosm.	2
Smilacaceae	*Smilax excelsa* L.	W(L)	FACW	CE	1,7
Typhaceae	*Sparganium emersum* Rehmann	H	OBL	Hol.	1,2,3,6,7
	Sparganium erectum subsp. *neglectum* (Beeby) K.Richt. (*S. neglectum* Beeby)	H	OBL	Pal.(W)	1
	Sparganium erectum L.	H	OBL	Pal.(W)	5
	Sparganium natans L. (*S. minimum* Wallr.)	H	OBL	Hol.	2
	Typha angustifolia L.	H	OBL	Hol.	1,2,4,5,6
	Typha latifolia L.	H	OBL	Cosm.	1,2,6,7
	Typha laxmannii Lepech.	H	OBL	Pal.	1

Out of the 218 plots, 65 were taken in seasonally dry areas (water not visible), 37 were taken in fully water-covered habitats (water well visible), 113 – partially water-covered habitats (water hardly visible) and for three plots no data. It should be noted that we canceled a certain number of plots since we found different types of agricultural fields in places where, according to the old Soviet maps, there should have been wetlands.

According to the degree of human impact on the habitat, 46 plots were assessed as low (insignificant or not observed at all), 82 plots were assessed as intermediate (low impact rate), 89 plots were assessed as high (high anthropogenic impact), and for one plot there was no data.

During the fieldwork, we recorded *Drosera rotundifolia* for the first time in the Samegrelo region, where, together with the *Rhynchospora alba*, they make a unique plant community in the middle of the urbanized area (village Namikolaevo). This location is not mentioned for this species in the 'Flora of Georgia' (Ketskhoveli et al. 1971-2011), nor in the other reviewed literature. Regretfully, this unique habitat is in a very poor state owing to grazing by domestic animals and fragmentation, and it is possible that without proper protective measures it will disappear soon (see Suppl. material 2, fig. 5).

The presence of FAC and FACU species among the ten most frequently occurring species, the relatively low level of endemism against a high percentage of non-native species, and the assessment of 89 out of 218 sites as being under heavy human influence are indicative of the current challenging status of wetlands. The remaining undamaged wetlands with their highly diverse vegetation, distinctive relics, unique flora, and picturesque landscapes are impressive and can attract many visitors, provided such recreational and touristic activities are duly organized.

CCA axis 1 explained 63% of the variation in species distribution along geographical gradients, this axis was statistically highly significant ($p = 0.005$). The second axis explained 37% of this variation, yet it was insignificant ($p = 0.34$). Axis 3 could be dismissed as its explanatory power was very low (less than 1%, $p = 0.53$). The triplot (Fig. 2) shows that axis 1 represents variation in altitude and longitude. Variation in latitude apparently does not play an important role as it is associated with the insignificant axis 2. Altitude in Georgia is tightly correlated with the mean annual temperature and can serve as its precise proxy, whils longitude can be a proxy of precipitation (Kikvidze 2020). Therefore, perhaps the main climatic driver of species composition in the wetlands of Georgia is temperature, while precipitation might play a secondary role since the main feature of the wetlands is waterlogging, which can only weakly depend on precipitation.

Summary

Our study presents the most comprehensive checklist of Georgia's wetland flora compared to any previously published work. Importantly, we added an assessment of an indicator status, life forms, and chorotypes to each species, and the coordinates to each site in supplementary data in the form of a presence-absence matrix. The present list of plant species is based only on the results of field studies. The checklist includes 270 species belonging to 80 families and 183 genera. Among them are some non-native species that are not yet included in the 'Flora of Georgia' (e.g., *Eucalyptus cinerea*, *Pinus pinaster*, and *Hibiscus coccineus*). Angiosperms are the core of the floristic composition – 251 species (93%). Bryophytes are represented by 10 species (3.7%), Pteridophytes – 8 (3%), Gymnosperms – 1 (0.4%). Leading families by the number of species are Cyperaceae – 39 (14.4%), Poaceae – 29 (10.7%), Rosaceae – 19 (7.1%), Asteraceae – 17 (6.3%), Fabaceae – 11 (4.1%), and Juncaceae – 11 (4.1%). The floristic composition of Georgian wetlands is dominated by Palaearctic species 55 (20.4%), followed by Holarctic 46 (17.1%), Euro-Mediterranean 31 (11.5%), Cosmopolitan 31 (11.5%) and Euro-Siberian 27 (10.03%) species. Endemism is 4.8% and the proportion of invasive and naturalized plants is 8.5%. Obligate wetland plants, mainly belonging to the families Cyperaceae and Juncaceae, make up 34.2% of the floristic composition. Out of 270 species, half are represented

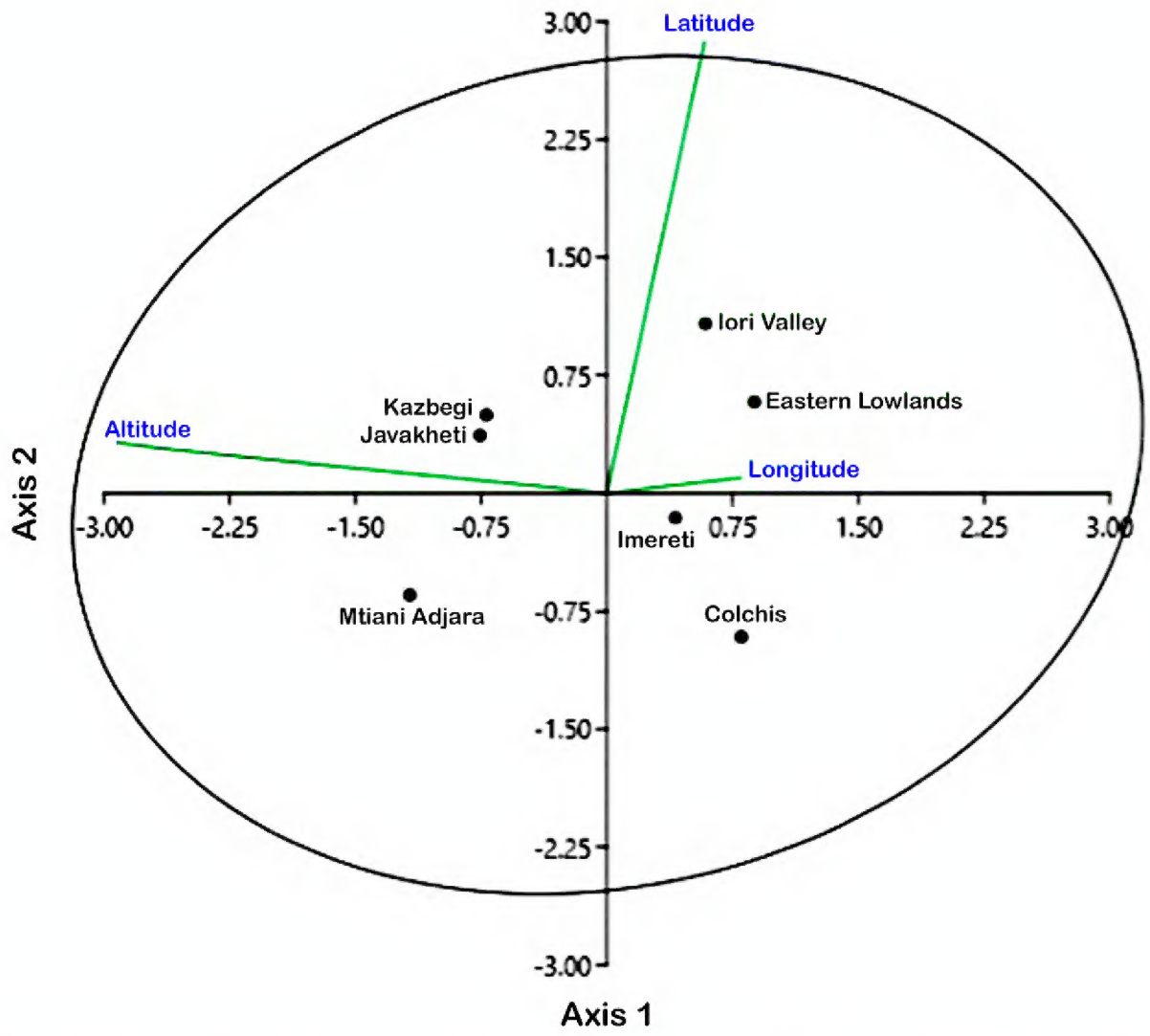

Figure 2. Wetland vegetation species composition along geographical gradients as analyzed with the CCA ordination; all data are well within the 95% confidence interval (encircled). "Eastern lowlands" include the wetlands in Shida Kartli Lowland and Alazani Valley; Iori Valley stands for the entire Iori River gorge.

by only one or two sites. The five most frequent species are *Alnus glutinosa* subsp. *barbata*, *Molinia caerulea*, *Juncus effusus*, *Carex vesicaria* and *Phragmites australis*. 52.1% of species belong to the OBL and FACW categories. Therefore, the main climatic driver of species composition in the wetlands of Georgia seems to be temperature, while precipitation plays a secondary role since the main feature of the wetlands is waterlogging, which can only weakly depend on precipitation.

Overall, our results indicate that the wetlands are under strong anthropogenic influence. We hope that this checklist will facilitate further work on completing the Georgian wetlands plant inventory.

დასკვნა

ჩვენი კვლევა წარმოადგენს საქართველოს ჭარბტენიან ჰაბიტატებში გავრცელებული სახეობების ყველაზე სრულ ნუსხას ადრე გამოქვეყნებულ შრომებთან შედარებით. რაც მთავარია, ჩვენ თითოეულ სახეობას მივანიჭეთ ჭარბტენიანი ტერიტორიების ინდიკაციის სტატუსი, სასიცოცხლო ფორმები და ქოროტიპები. ასევე მოცემულია თითოეული სახეობისთვის გავრცელების კოორდინატები ყოფნა-არყოფნის მატრიქსის სახით. ამასთან, მცენარეთა სახეობების არსებული სია ეყრდნობა მხოლოდ ველზე ჩატარებული აღწერების შედეგებს. ნუსხა მოიცავს 270 სახეობას, რომელიც გაერთიანებულია 80 ოჯახსა და 183 გვარში. ენდემიზმის პროცენტული მაჩვენებელი შეადგენს 4.8 %-ს, ხოლო ინვაზიური დანატურალიზებული სახეობები შეადგენს 8.5%-ს. ჭარბწყლიანი გარემოსთვის დამახასიათებელი სახეობები შეადგენს საერთო რაოდენობის 34.2%-ს და ძირითადად მიეკუთვნება Cyperaceae და Juncaceae-ს ოჯახებს.

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Author contributions

GM planned the research; GT, GM, IA, NM, VM and ZJ conducted the field sampling; GT and TJ harmonized the nomenclature of species with international databases; GT and NL defined chorotypes; ZK performed the statistical analyses and led the writing; all authors critically revised the manuscript.

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Supplementary material 1

Images of some rare wetland species in Georgia

Authors: Tedoradze G 2023
Data type: image
Explanation note: Images of some rare wetland species in Georgia are given, including *Drosera rotundifolia, Rhynchospora alba, R. caucasica, Salvinia natans,* and *Trapa natans*.
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Link: https://doi.org/10.3897/caucasiana.2.e101677.suppl1

Supplementary material 2

Some wetland panoramas from different regions in Georgia

Authors: Tedoradze G 2023
Data type: image
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Link: https://doi.org/10.3897/caucasiana.2.e101677.suppl2

Supplementary material 3

Some characteristic wetland species in Georgia

Authors: Tedoradze G 2023
Data type: image
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Link: https://doi.org/10.3897/caucasiana.2.e101677.suppl3

Supplementary material 4

Coordinates of sampling sites, wetland characteristics

Authors: Tedoradze G et al. 2023
Data type: species data
Explanation note: Coordinates of sampling sites, wetland characteristics (such as water cover and anthropogenic impact), and presence-absence data for all plant species given in the check-list are provided.
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Link: https://doi.org/10.3897/caucasiana.2.e101677.suppl4